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A Late Permian Captorhinid from Rhodesia

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ABSTRACT

Two partial skulls from the late Permian Madumabisa Mudstone in the Middle Zambezi Basin of Rhodesia belong to the captorhinid genus *Protocaptorhinus*. Heretofore, *Protocaptorhinus* has been known only from the Early Permian of Texas, whereas Africa has yielded only one other captorhinid, *Moradisaurus*, from Niger. The Captorhinidae is a monophyletic group (possibly including turtles) with these derived characters: downturned premaxilla, ectopterygoid and tabular absent, medial process of jugal. *Protocaptorhinus* differs from *Romeria* in having a shallow median parietal embayment and differs from remaining captorhinids in lacking a retroarticular process.

INTRODUCTION

In May 1976, Mr. Brian Hosking and the junior author made a small collection of therapsid and captorhinid skulls from a late Permian locality in Rhodesia. The two captorhinid specimens are of particular interest because they provide the second record of this group from Africa. The captorhinid skulls have been identified as *Protocaptorhinus*, a form previously known only from the Early Permian of North America. The Captorhinidae is usually placed in the Captorhinomorpha, an avowedly paraphyletic group that is generally considered to contain the ancestors of later amniotes. This situation has prompted a phylogenetic study of the Captorhinidae using shared derived characters (see Gaffney, 1979, for a discussion of the methodology used here).

Previous work on captorhinids and captorhinomorphs in general has been summarized in Kuhn (1969), but the papers that are the most pertinent to this study are Clark and Carroll (1973) and Heaton (1979).

The junior author provided the geologic and locality information (as well as the specimens), and the senior author is alone responsible for the morphology and discussion sections.

ACKNOWLEDGMENTS

We are particularly indebted to Dr. Robert Carroll, McGill University, Montreal, and Drs. Malcolm Heaton and Robert Reisz, Erindale University, Toronto, for sharing their specimens and unpublished data, and for examining our material and providing us with some very useful ideas. Dr. Heaton gave us free access to his thesis on *Eocaptorhinus* which, at that time, was still unpublished. The very difficult preparation of the specimens was accomplished by

Mr. Gil Stucker using an air abrasive machine. Mr. Chester Tarka and Ms. Lorraine Meeker produced the illustrations.

We also thank Professor G. Bond and Mr. Brian Hosking of the Geology Department, University of Rhodesia, for their hospitality and logistic support of the junior author, both in Salisbury and in the field. Dr. Raath, formerly Director of Museums and Monuments of Rhodesia, now at the Bernard Price Institute, Johannesburg, generously arranged for permission to collect and for the loan of specimens for study. Dr. C. B. Cox, University of London, King's College, identified the associated anomodont material.

ABBREVIATIONS

INSTITUTIONS
OU, University of Oklahoma
QG, National Museums of Rhodesia
ANATOMICAL

ang, angular	pfr, prefrontal
art, articular	pm, premaxilla
bo, basioccipital	po, postorbital
den, dentary	ps, parasphenoid
fr, frontal	pt, pterygoid
ju, jugal	qj, quadratojugal
la, lacrimal	qu, quadrate
mx, maxilla	sm, septomaxilla
na, nasal	sq, squamosal
pa, parietal	st, supratemporal
pal, palatine	vo, vomer
pf, postfrontal	

SYSTEMATICS

FAMILY CAPTORHINIDAE

Protocaptorhinus Clark and Carroll, 1973

Protocaptorhinus, sp.

SPECIMENS: QG 1105, anterior portion of skull; QG 1106, posterior portion of skull (see figs. 1-3).

LOCALITY: Small patch of badlands lying at the base of a large hill just south of the confluence of the Sengwa and Lutope rivers, 18°07′ S. latitude, 28°12′ E. longitude[1]; Gokwe Tribal Trust Area, Middle Zambezi Basin,

[1] UTM grid reference PL283009 on 1:50,000 series of Rhodesia, sheet 1828A.

Rhodesia. Fossils occur in sideritic concretions forming a lag concentrate.

HORIZON: Middle Madumabisa Mudstones, K^{5d} of Bond (1973); late Permian (Dzhulfian) in age. The captorhinids were found associated with therapsids, most of which are endothiodonts similar to *Emydops* (C. B. Cox, personal commun.).

COLLECTORS: Malcolm C. McKenna and Brian Hosking, May 1976.

DESCRIPTION

Among the captorhinid taxa used for comparisons here, *Captorhinus* and *Eocaptorhinus* are by far the best known, being represented by a number of well-preserved skulls. Price (1935) and Fox and Bowman (1966) have produced descriptions of *Captorhinus*, and Heaton (1979) has described *Eocaptorhinus* in even greater detail. Considering that the two taxa differ only in the number of tooth rows (providing that one accepts the hypothesis that they are different at all), this skull type is as well known as any Recent form. *Romeria* and *Protocaptorhinus*, however, are known from three and two skulls, respectively, all of which lack significant portions of the palate (Clark and Carroll, 1973). The currently known material of *Romeria* and *Protocaptorhinus* and the excellent specimens of *Captorhinus* and *Eocaptorhinus* were available for comparison with the Rhodesian *Protocaptorhinus* during the course of this study. In many cases comparisons had to be restricted to *Captorhinus* and *Eocaptorhinus* because of the poor preservation of *Romeria* and *Protocaptorhinus* specimens. In the following description, *Protocaptorhinus* always refers to the North American material, the Rhodesian skulls are not identified as *Protocaptorhinus* until the Discussion section.

SKULL

PREMAXILLA: The premaxilla is best seen on the right side of QG 1105 where only a portion of the internarial region is badly damaged. The preserved areas agree closely with *Captorhinus* and *Eocaptorhinus* as described by Fox and Bowman (1966) and Heaton (1979). Although

all the premaxillary teeth are damaged to some extent, it does seem clear that each bone has four teeth. *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus* have four or five premaxillary teeth and a distinct size gradation in these teeth with the anteriormost being longest and widest and the posteriormost being shortest and smallest. The Rhodesian specimen is consistent with these characters but the anteriormost tooth does not seem to be relatively as large as that seen in the North American taxa.

MAXILLA: Both maxillae are preserved in QG 1105, but the left maxilla is somewhat crushed. The external limits and shape of the maxilla agree with that seen in *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus*. The anterior limit of the maxilla forms part of the narial margin, there is a mid-length dorsal swelling, and a posterior jugal contact; all as in the New World forms. The mid-length swelling coincides with the position of the largest maxillary teeth, some of which may become distinctly larger than the other maxillary teeth. The Rhodesian form, however, has maxillary teeth that are somewhat more similar to each other in size and conspicuously enlarged caniniform teeth are absent. Bolt and De Mar (1975) noted some variation in this feature in *Captorhinus*.

The lower jaws have not been removed from the skulls of the Rhodesian specimens but it is possible to determine that a single row of teeth is present as in *Protocaptorhinus* and *Eocaptorhinus*.

The number of maxillary teeth is in doubt because of the presence of the lower jaws, but on the right side 19 maxillary teeth are visible, whereas the damaged left side shows evidence of a minimum of 12 teeth. Heaton (1979) reported 17 to 22 teeth in *Eocaptorhinus*, and Clark and Carroll (1973) stated that *Protocaptorhinus* had 18 to 22. Although the Rhodesian material is not well enough preserved to resolve the matter, it does seem that as many as five gaps may be present in the right tooth row that may represent damaged or lost teeth or replacement pits. Twenty-one tooth positions are indicated in the restoration as a conservative estimate.

SEPTOMAXILLA: Although one was presumably present, the septomaxilla is not visible.

LACRIMAL: The lacrimal is preserved best on the right side of QG 1105 and extends from the anterior edge of the orbit to the posterior edge of the nares. It compares closely with *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus*.

NASAL: The limits and dorsal surface of the right nasal are clearly preserved in QG 1105 although the area bordering the nares is somewhat damaged. The left nasal is broken and crushed but agrees in morphology with the right. The only distinction between the nasal of the Rhodesian skull and *Captorhinus* is the slightly more extensive prefrontal contact and less extensive lacrimal contact in the former.

PREFRONTAL: The prefrontal in QG 1105 is badly damaged on the left side, but complete on the right. It forms the border of the orbit anterodorsally and extends forward to separate the nasal and lacrimal for much of their lengths. It agrees in detail with *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus*.

FRONTAL: The frontal is best seen in QG 1105 but fragments of it as well as the frontoparietal suture are preserved in QG 1106. The frontal agrees closely with *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus*.

PARIETAL: QG 1106 has a complete right parietal and portions of the left preserved but the posteromedial surface is damaged making the midline parietal suture and the pineal foramen impossible to determine. The parietal in the Rhodesian form differs slightly from *Protocaptorhinus*, *Captorhinus*, *Eocaptorhinus*, and romeriids in apparently having a medial constriction about midway along its length. Also, as restored here, the proportions of the parietal are somewhat closer to those seen in *Romeria* (Clark and Carroll, 1973) in that the length and width are about the same rather than the length being slightly greater than the width as in *Captorhinus*. However, this difference may very well be within the margin of error in the restoration due to preservational artifacts and to the absence of a distinct midline suture to maintain control of symmetry. The posterior margin of the parietal lacks the occipital em-
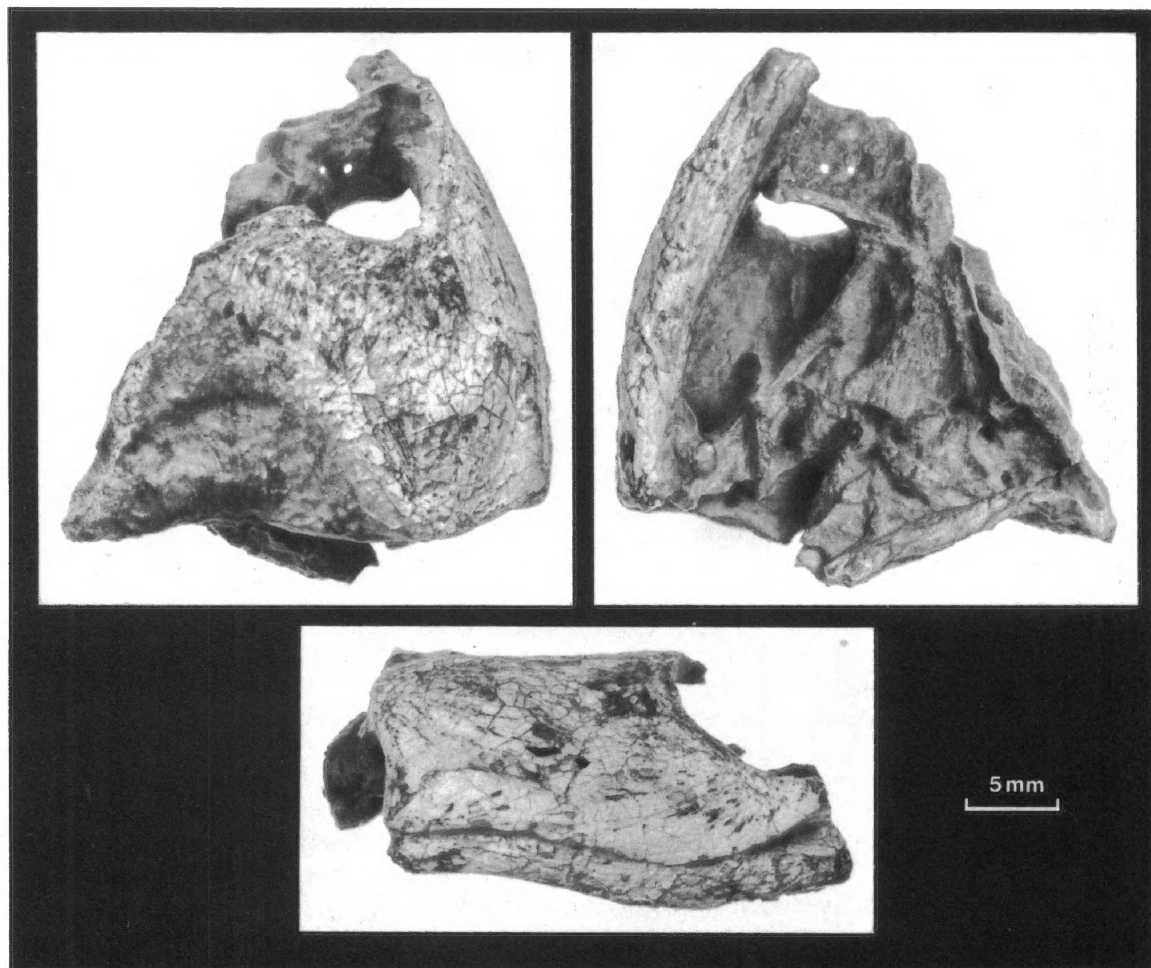
FIG. 1. *Protocaptorhinus* sp., QG 1106, Late Permian, Rhodesia. Posterior skull portion in dorsal (upper left), ventral (upper right), and right lateral (lower) views.

bayment seen in *Romeria* and has the truncated morphology seen in *Protocaptorhinus*, *Captorhinus* and *Eocaptorhinus*.

POSTPARIETAL: The occiput is known only in QG 1106 and although the presence of postparietals is clear their shape is not. What is present is consistent with *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus*.

SUPRATEMPORAL: The area where the supratemporal lies is badly broken. The lateral limits are clear but the medial ones are not. Although the occipital area is poorly preserved, there is no indication of a tabular.

POSTORBITAL AND POSTFRONTAL: Both bones are preserved in their entirety only on the

right side of QG 1106; QG 1105 retains only the anterior regions of the two elements. The bones as preserved agree closely with the postorbital and postfrontal of *Protocaptorhinus*, *Captorhinus*, *Eocaptorhinus*, and *Romeria*.

JUGAL: The jugal is present on the right side of both skulls; QG 1105 lacks the posterior margin of the bone while QG 1106 lacks the anterior process. As in *Romeria*, *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus* the anterior process of the jugal tends to separate the lacrimal and maxilla for a short distance. The posterior, expanded plate of the jugal also agrees with those taxa.

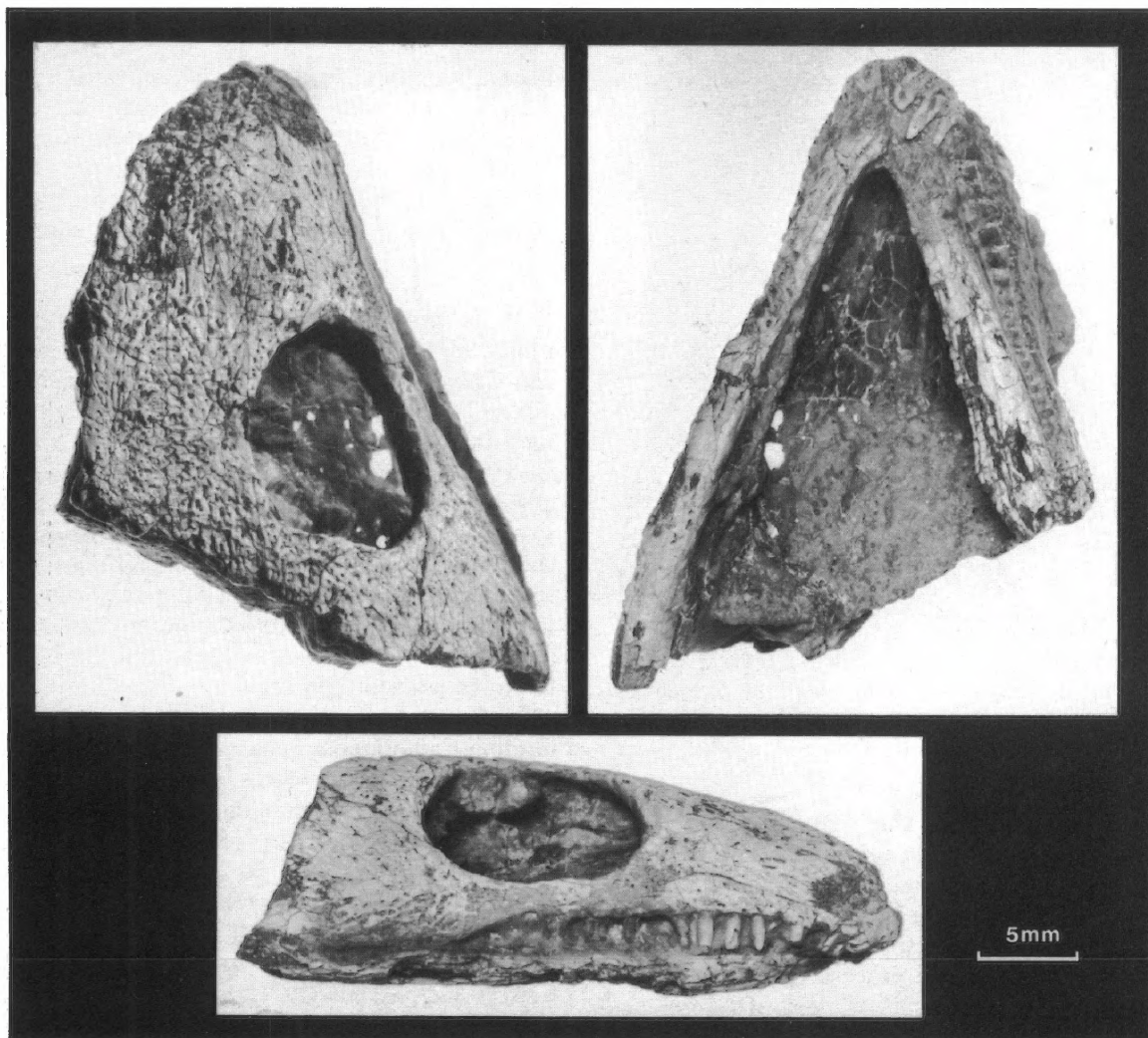SQUAMOSAL: The squamosal is present only

FIG. 2. *Protocaptorhinus* sp., QG 1105, Late Permian, Rhodesia. Anterior skull portion in dorsal (upper left), ventral (upper right), and right lateral (lower) views.

on the right side of QG 1106. The bone agrees with that element in *Protocaptorhinus*, *Captorhinus*, and *Eocaptorhinus* except for the slight medial extension along the parietal suture. As mentioned under Parietal this distinction in shape of the parietal-squamosal suture between New World forms and the Rhodesian form may be due to errors in the restoration. The posterior flange of the squamosal is partially preserved on the right side but so badly damaged that its original extent cannot be seen.

QUADRATOJUGAL: As in *Protocaptorhinus* and *Romeria* the quadratojugal of the Rhode-

sian form is somewhat convex upward rather than straight as in *Eocaptorhinus*.

PALATE AND BRAINCASE

The palate and braincase in both Rhodesian specimens are poorly preserved; the general features are determinable but many sutures and other structures are dubious. Furthermore, the palate in the two known specimens of North American *Protocaptorhinus* is even less informative, restricting comparisons to *Romeria*, *Eocaptorhinus*, and *Captorhinus*. In all deter-
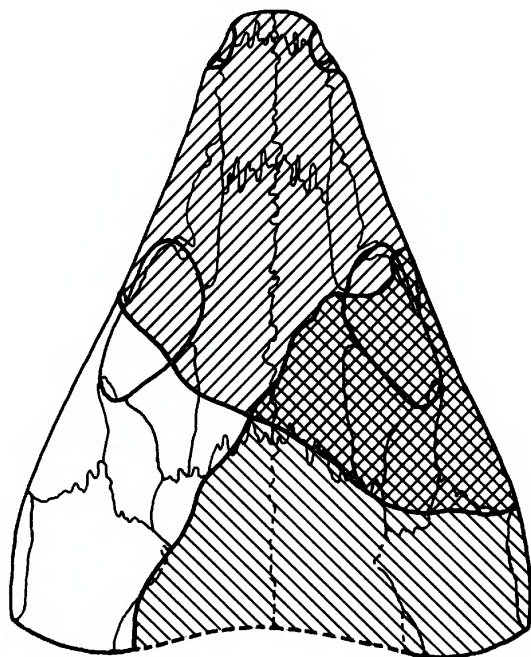
FIG. 3. Diagram showing extent of overlap and portions represented by the two skulls of *Protocaptorhinus* from Rhodesia.

minable features of the palate the Rhodesian forms agree with *Eocaptorhinus*. Two important features diagnostic of the Captorhinidae of Heaton (1979) are the medial jugal process and the absence of the ectopterygoid. What appears to be a medial jugal process is present in QG 1106 but its limits are not clear. The presence or absence of an ectopterygoid cannot be determined.

MANDIBLE

The anterior portions of the lower jaws are preserved in QG 1105, whereas the right side of QG 1106 has the posterior half present. The lower jaws are tightly clenched and crushed dorsally preventing any view of the teeth but the broken section on QG 1105 shows that a single tooth row was present at that position. As in other members of Group 2 (fig. 6), the prearticular forms a horizontal, medially directed process. In the Rhodesian material, however, the process ends in a small nubbin rather than a flat plate.

The primary area of systematic interest in the lower jaw is posterior to the quadrate articulation. *Captorhinus* and *Eocaptorhinus* (Group 2 in fig. 6) characteristically possess a well-developed retroarticular process that is not found in *Protocaptorhinus* and *Romeria*. QG 1106 has this region well preserved and clearly shows that a retroarticular process was absent.

DISCUSSION

It is apparent that the Rhodesian skull is nearly identical to a form described by Clark and Carroll (1973) from the Lower Permian of Texas as *Protocaptorhinus pricei*. As can be seen in table 1 the Rhodesian form and *Protocaptorhinus* do not differ in any features usually deemed significant in captorhinomorph systematics and, because of this, the Rhodesian skull is here identified as *Protocaptorhinus* sp. In order to ascertain just what this might mean it is necessary to inquire into the phylogenetic relationships of *Protocaptorhinus* and the Captorhinomorpha in general.

The group of amniotes arrayed under the heading Captorhinomorpha are characterized by the possession of features usually considered plesiomorphic for Amniota. Few, if any, authors have argued for strict monophyly of Captorhinomorpha, and the general consensus of most fossil reptile workers is that the group includes the ancestors of all reptiles, by definition if not by fact. For example, according to Carroll and Gaskill (1971, p. 450): "The suborder Captorhinomorpha occupies a central position in the phylogeny of reptiles. Within the group are the ancestors of most, if not all, more advanced members of the class." The Captorhinomorpha is one of the classic "primitive" or "ancestral" groups set up for supposed taxonomic convenience that has actually impeded the development of ideas about the relationships of the contained taxa by covering them with a cloak of taxonomic respectability. The lower level taxa referred to the Captorhinomorpha have been relatively consistent from the time of Watson's (1917) first delimitation of the assemblage, that is, *Captorhinus* and other taxa that are morphologically similar. Watson diagnosed Captorhinomorpha as "cotylosaurs [i.e., anapsids] with an obliterated

otic notch and vertically placed quadrates" (p. 172). These features are found widely throughout the Amniota and are presumably primitive for that group or a large subsection of that group.

Within the Amniota strict monophyly for Synapsida (Theropsida), Diapsida, and Testudines is assumed for the purposes of this discussion, but even ignoring fossil groups such as Euryapsida, does not aid in the development of restricted outgroups or a higher level phylogenetic system within the Amniota. In order to test rigorously hypotheses of relationship for forms placed in the Captorhinomorpha some well-tested higher level system is needed within Amniota, but it is not available. The closest thing to it is Goodrich's (1916) Sauropsida and Theropsida, each of which are characterized by a uniquely derived aortic arch condition. The Sauropsida would contain Testudines and Diapsida as the sister group of Synapsida. However, Parsons's (1959) demonstration that all living amniotes, except turtles, have a Jacobson's organ (as delimited by him) and that there is no evidence that non-amniotes or turtles ever had one, contradicts the Sauropsida and supports the idea of turtles as the sister group of a monophyletic Diapsida plus Synapsida. More work on this problem clearly is necessary and until we have some well-tested higher level phylogenies within the Amniota, phylogenetic work within such paraphyletic groups as Captorhinomorpha will be very tentative at best. Nonetheless, some ideas can be formulated so that they are more susceptible to tests using synapomorphies.

Clark and Carroll (1973) and especially Heaton (1979) presented a phylogeny of *Protocaptorhinus* and its near relatives. They utilized a systematic methodology that is near that characterized by Gingerich (1976) as "stratophenetic." In this methodology, similar morphologies are arranged stratigraphically and connected using usually implicit rather than explicit criteria, to form what are interpreted as ancestor-descendant lineages. Clark and Carroll presented such a phylogeny (1973, fig. 21) and remarked (*ibid.*, p. 392): "Although much more remains to be done in preparing and illustrating the material, it definitely demonstrates a long and gradual evolution of the typical captorhinid features from the romeriid pattern." Heaton (1979, p. 81) stated: "The sequence of *Romeria-Protocaptorhinus-Eocaptorhinus-Captorhinus* is interpreted as a single continuous phylogenetic lineage. . . ." This type of approach to phylogeny reconstruction has been effectively criticized (Engelmann and Wiley, 1977; and more particularly McKenna, Engelmann and Barghoorn, 1977) and Heaton's phylogeny (which is virtually the same as Clark and Carroll's) is reformulated here in more objective terms as a potentially testable hypothesis.

Heaton's phylogenetic tree is one of several that are consistent with a single cladogram (fig. 6). Testing this cladogram using unique derived character distributions (synapomorphies or derived characters) is difficult, because of the higher level phylogeny problems indicated above, but not impossible. Actually, a greater difficulty is one of diagnosing the basic taxa used in such a study because of Carroll's and Heaton's adherence to the stratophenetic method. In this method, the determination of generic and specific level taxa generally follows the "recognition" of phylogenetic sequences in the rock column and the resultant taxa are not intended to be strictly monophyletic nor distinguishable solely by morphology in the absence of stratigraphic information.

In the cladogram presented here, Group 1 is effectively the Amniota, although quite a few taxa are missing. Amniota has the following synapomorphies: pterygoid flange and astragalus (see Gaffney, 1979, for discussion). Nearly all the missing taxa would be exclusive of Group 2; only turtles might be members of Group 2. The Captorhinomorpha is considered by Clark and Carroll (1973) to consist of the "Romeriidae" and Captorhinidae.[1]

The two best known romeriids are *Paleothyris* from the Middle Pennsylvanian of

[1]Heaton and Reisz (MS.) diagnose the "Romeriidae" (which they call by its more apt name, Protothyrididae) and the Captorhinidae. They attempt to diagnose these taxa using primitive and advanced features and the reader should refer to their paper because it preempts much of the above discussion on the "Romeriidae."
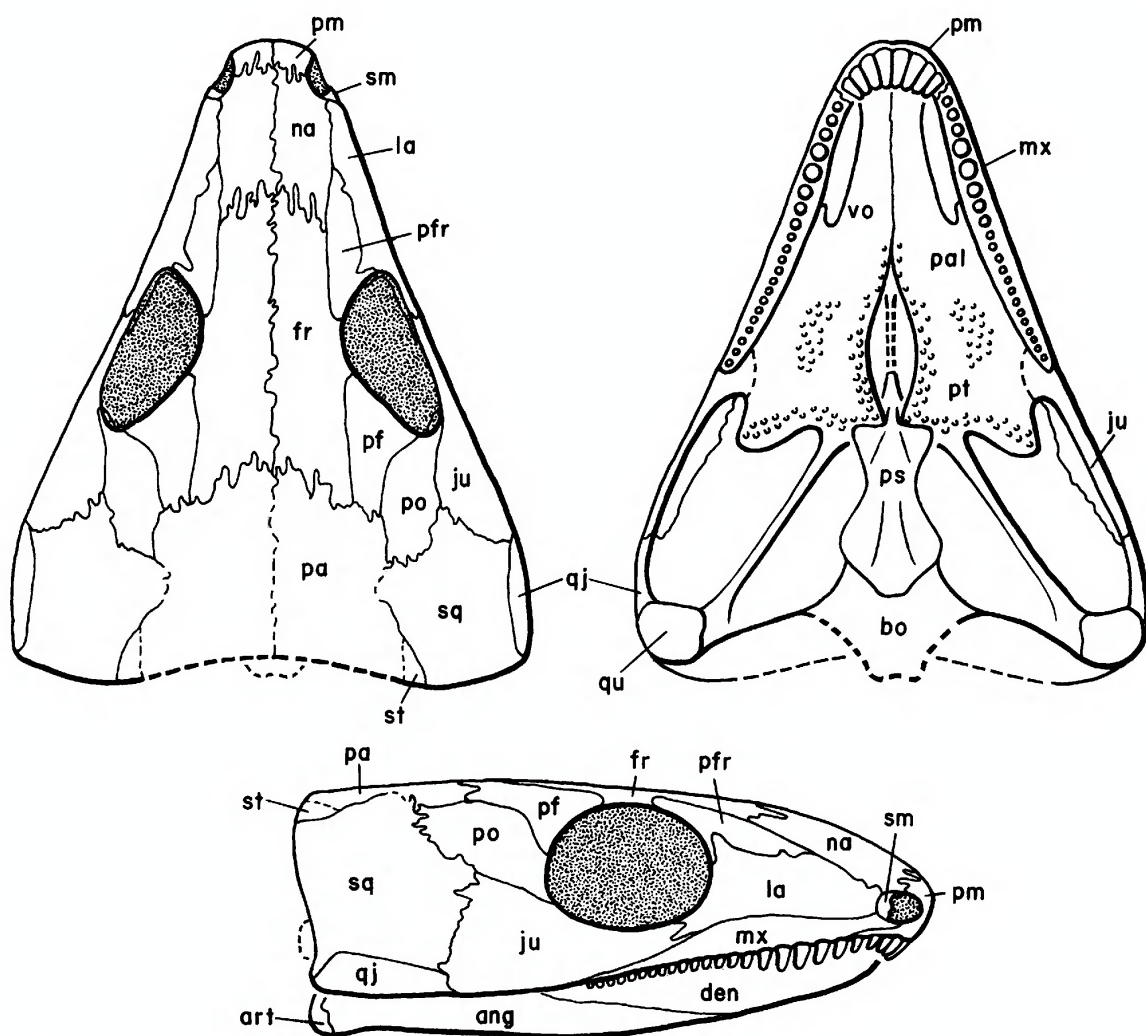
Fig. 4. *Protocaptorhinus* sp., Late Permian, Rhodesia. Reconstruction of skull based on QG 1105 and QG 1106.

Nova Scotia and *Protorothyris* from the Lower Permian of Texas and West Virginia, recently described by Carroll (1969) and Clark and Carroll (1973). According to Clark and Carroll (*ibid.*, p. 400): "Of all known groups of Paleozoic reptiles only romeriids are sufficiently generalized to be ancestral to any of the subsequent lineages." Within the romeriids, *Paleothyris* and *Protorothyris* are primitive in nearly all characters used in captorhinomorph systematics and, to put Carroll's ideas in cladistic terminology, they may be hypothesized as the plesiomorphic sister taxon to nearly all Amniota. Although Carroll is the leading contemporary student of the "Romeriidae" and has produced excellent descriptions of members of the group, he has not published a diagnosis of this family, nor has Heaton, who recently altered the contents of the family by removing *Romeria* from it. Romer's (1956) diagnosis rested primarily on *Romeria* and *Protorothyris*. If we use the taxa placed in the "Romeriidae" by Carroll and Baird (1972) and Clark and Carroll (1973) but minus *Romeria*, we seem to have the following features necessary for inclusion in the group:
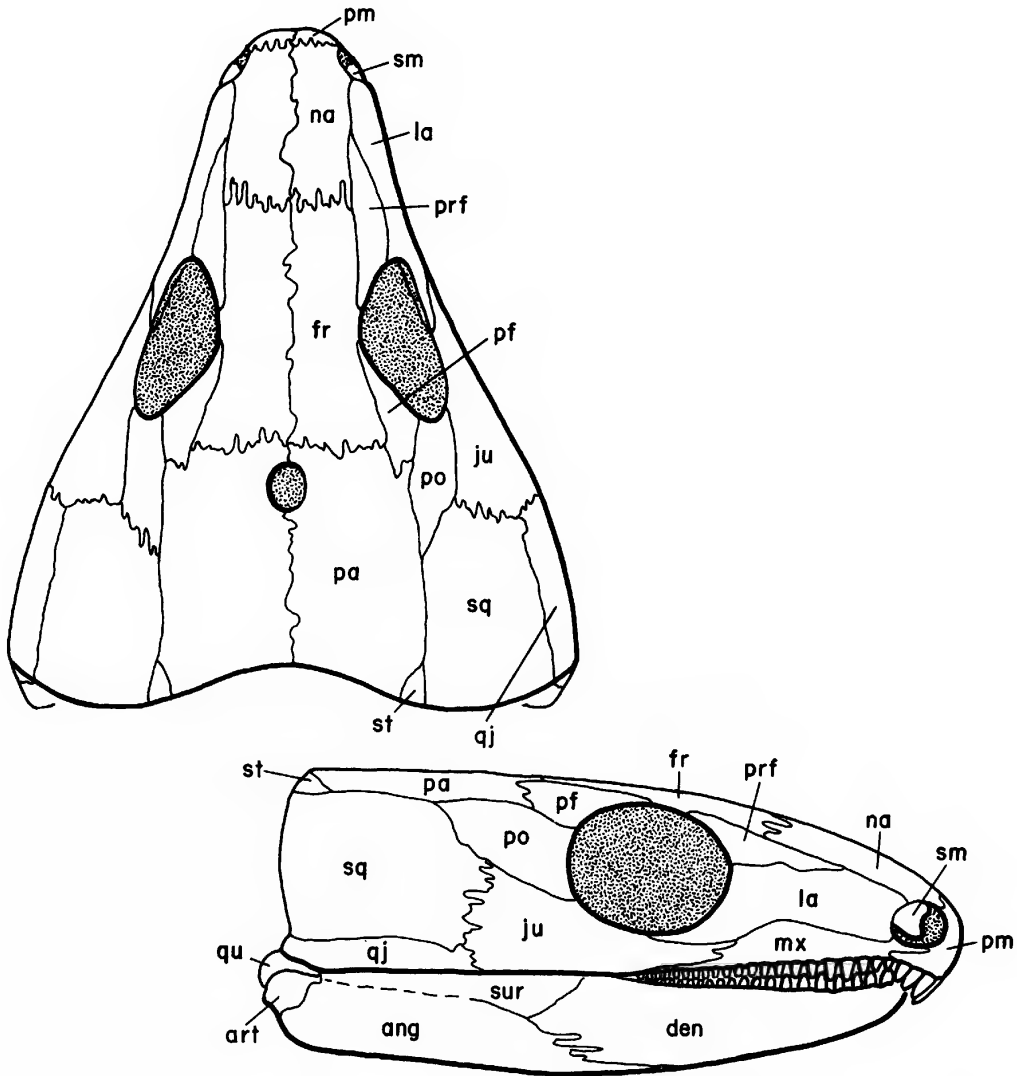
FIG. 5. *Captorhinus aguti*, Early Permian, Ft. Sill, Oklahoma, University of Kansas 9978.

1. Characters derived for Amniota such as a transverse pterygoid flange.
2. Large squamosal broadly covering posterior margin of cheek, forming an upright or nearly vertical skull margin, no otic notch.
3. Small, splintlike supratemporal usually inserting into a posterolateral lappet of the parietal, not contacting postorbital.
4. Tabular and postparietal small, restricted to occipital surface.
5. Lacrimal extends from nares to orbit.
6. Ectopterygoid present.
7. Lateral deflection of maxilla absent, lateral margin of skull forms nearly straight line in dorsal view.
8. Maxillary tooth row straight in lateral view.
9. Jugal lacks medial process.
10. Moderate bilateral parietal embayment along posterior margin.
11. Tooth row single in upper and lower jaws.
12. Retroarticular process of lower jaw absent.
13. Quadrate low, largely covered externally by squamosal and quadratojugal.

All of these characters seem to be primitive for Amniota and none is unique to the
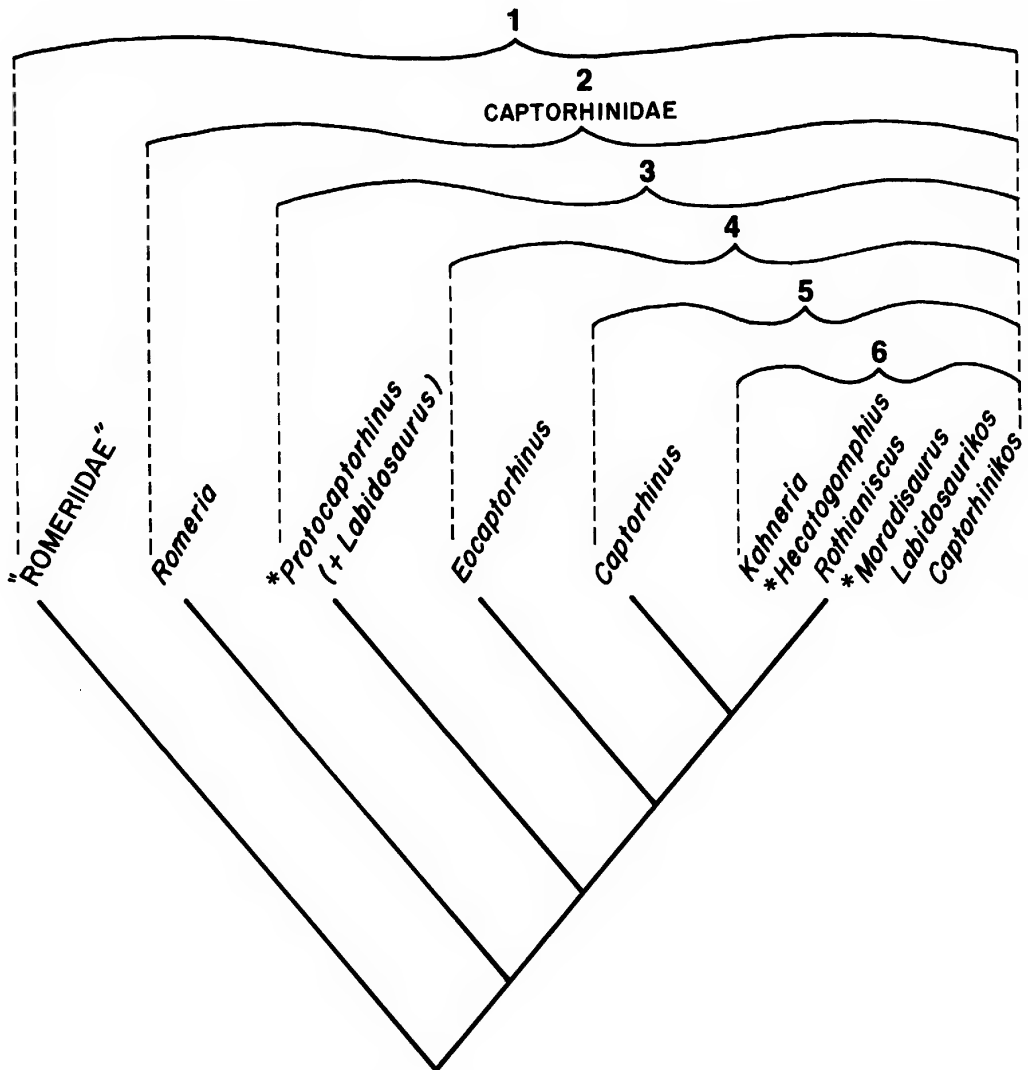
FIG. 6. Cladogram of Captorhinidae. Numbers refer to groups discussed in text. Asterisks indicate taxa that occur outside North America (*Protocaptorhinus* also occurs in North America). *Labidosaurus*, although a distinct genus, fits in the cladogram at the same position as *Protocaptorhinus*.

"Romeriidae," which is not surprising for an intentionally paraphyletic group.

Group 2 is the Captorhinidae of Heaton (1979), which equals the Captorhinidae plus *Romeria* of Clark and Carroll (1973). This difference in familial content lies in the fact that Group 2 is more readily characterized and distinguished than the Captorhinidae of Clark and Carroll (1973) and, to the stratopheneticist, it is delimited by a marked break in the perceived

"continuum." Clark and Carroll (1973, p. 399) believed that "This point of division has, however, the lamentable taxonomic implication of removing the type genus from the family "Romeriidae". Since the name Romeriidae has long been associated with the phylogenetically most important family of Paleozoic reptiles and also honours one of this century's greatest contributors to vertebrate paleontology, an alternative point of separation should be considered."

TABLE 1
Comparison of Cranial Features in Romeriidae and Captorhinidae

	Paleothyris	Protorothyris	Romeria	North American Protocaptorhinus	Rhodesian Protocaptorhinus	Labidosaurus	Eocaptorhinus	Captorhinus	Group 6[a]
Posterior parietal embayment	bilateral, shallow	bilateral, deep	bilateral, deep	median, shallow	median, shallow	median, shallow	median, shallow	median, shallow	median, shallow
Tabular	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Downturned premaxilla	Absent	Absent	Present	Present	Present	Present	Present	Present	Present
Ectopterygoid	Present	Present	Absent (?)	Absent (?)	Indeterminate	Absent	Absent	Absent	Absent
Medial process of jugal	Absent	Absent	Present (?)	Present (?)	Present (?)	Present	Present	Present	Present
Retroarticular process	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
Number of tooth rows	One	One	One	One	One	One	One	Two-three	four-nine

[a]See figure 6 and text for contents.

In a cladistic classification such a situation would not be a problem; by choosing the correct level for its application, 90 percent of amniotes could be placed in the "Romeriidae" in order to make it monophyletic. In any case, Heaton makes his division excluding *Romeria* from the "Romeriidae", and this is followed here because *Romeria* has the characters of Group 2.

Group 2, the Captorhinidae, has these features that we interpret as synapomorphies:

1. Downturned premaxilla
2. Medial process of jugal
3. Ectopterygoid absent
4. Tabular absent

A downturned premaxilla occurs in various amniote groups but the only group in which it appears to be primitive is the turtles. Pelycosaurs, some therapsids, and turtles have a medial jugal process but only turtles lack an ectopterygoid. The presence of a tabular seems to be primitive for diapsids as it occurs in *Youngina* and *Petrolacosaurus*, but it is absent in euryapsids. Synapsids have a well-developed tabular, but turtles do not. For the purposes of this study, I will accept Group 2 as a monophyletic group that may include turtles.

Group 3 is characterized by the absence of the distinctive bilateral parietal embayment seen in *Romeria* and *Protorothyris* and instead has a straight posterior margin or a margin with a slight median concavity rather than bilateral ones. Group 3 contains as sister taxa to Group 4 *Protocaptorhinus* and *Labidosaurus*. *Protocaptorhinus* is a monospecific genus described on the basis of two skulls by Clark and Carroll (1973) with additional data by Heaton (1979), whereas *Labidosaurus* although known for many years (Williston, 1910, 1917) has never been thoroughly described and compared.

Group 4 is advanced over the other taxa by the possession of a well-developed retroarticular process, a feature that has appeared many times in tetrapod history but, given the monophyly of Group 2, only once among these taxa. *Eocaptorhinus*, the sister taxon to Group 5, has recently been described by Heaton (1979) in a work that provides comparative morphology for many captorhinomorphs as well as an extremely detailed description of this form. *Eocaptorhinus* differs from *Captorhinus* solely in the possession of a single row of teeth rather than multiple rows as in *Captorhinus*. Bolt and De Mar (1975, p. 829) have shown that at the Fort Sill, Oklahoma, locality some specimens have a single tooth row on one side and a multiple row on the other and, therefore, question the validity of this character in diagnosing a new species. Heaton (1979) has discussed this problem and argues that *Eocaptorhinus* is a valid taxon. The question really revolves around paleontologic interpretations of the biologic species concept and, frankly, there is no real solution; rather the problem comes from "seeing" too much in the rocks. *Eocaptorhinus* is diagnosable using objective criteria; whether or not it is a "true" biologic species cannot be answered. On the other hand, if one chooses not to recognize *Eocaptorhinus*, then Group 4 and 5 are merged.

Group 5 has multiple tooth rows usually accompanied by some expansion of the tooth bearing elements. *Captorhinus aguti* is well known through the work of Price (1935) and Fox and Bowman (1966).

Group 6 contains the captorhinids with four or more tooth rows, and a distinctly large maxillary and mandibular tooth bearing surface. This group is of particular interest here because it includes all of the previously known extra North American records of captorhinids. Unfortunately, many of the included taxa are based on fragmentary material and none of them can be considered well known. *Captorhinikos* is the best known in the literature (Olson and Barghusen, 1962) and *Labidosaurikos* is represented by a well-preserved skull (UO 3-1-S2) so that the concept of this group presented here is based primarily on these two taxa.

The North American members of Group 6 include *Labidosaurikos*, its first-named member (Stovall, 1950). *Labidosaurikos* differs from *Captorhinus* in being larger, having six maxillary tooth rows and five mandibular tooth rows, and having a less well-developed retroarticular process, although one is present in contrast to *Protocaptorhinus*. *Captorhinikos* (Olson, 1954,

TABLE 2
Distribution of Captorhinidae[a]

	North America	Russia	Rhodesia	Niger	India
Late Permian (Tatarian/Ochoan)	—	—	*Protocaptorhinus*	*Moradisaurus*	presumed captorhinid
Middle Permian (Kazanian, Kungurian/Guadalupian)	*Kahneria* *Rothia*	*Hecatogomphius*	—	—	—
Early Permian (Artinskian, Sakmarian/Leonardian, Wolfcampian)	*Captorhinikos* *Labidosaurikos* *Labidosaurus* *Captorhinus* *Eocaptorhinus* *Protocaptorhinus* *Romeria*	—	—	—	—

[a]Romer (1973, p. 161) referred to a possible captorhinid from Tasmania, but in the absence of confirmation, I am ignoring it.

1970; Vaughn, 1958; Olson and Barghusen, 1962) is known from some good material but its differentiation from *Labidosaurikos* (as well as other Group 6 taxa) is principally on the basis of tooth arrangement and shape (Olson and Barghusen, 1962). *Captorhinikos* has a larger retroarticular process than *Captorhinus* and, in general, seems to agree with that form except in tooth row number.

Kahneria (Olson, 1962) and *Rothianiscus* (Olson and Beerbower, 1953; Olson, 1962, 1965) are Middle Permian Group 6 captorhinids known from somewhat damaged skulls that do not allow full comparison with other taxa. Both have four or five tooth rows and the typical expanded palatal and mandibular surfaces.

Kutty (1972) announced the presence of a captorhinomorph from the Permian of India associated with endothiodonts. On the basis of the endothiodonts Kutty suggested a correlation with the *Endothiodon* and *Kistecephalus* zones of South Africa, which would be Late Permian in age. Although the stratigraphic data leave something to be desired, the Indian form is placed in the Late Permian in the absence of contradictory information (table 2). The 9 cm.-long captorhinomorph skull was not described and only the dorsal view has been published as yet but the figure clearly shows features that

agree in detail with *Eocaptorhinus* and *Captorhinus*. In particular the strong lateral cheek deflection and the shallow median parietal embayment suggest identification with Group 3 but in the absence of information on other characters I am only identifying it as a captorhinid (Group 2).

The first discovered non-North American captorhinid was *Hecatogomphius* (Vyushkov and Chudinov, 1957; Olson, 1962), based on a lower jaw with five tooth rows that was found in Zone II of the Russian Permian (Late Permian). Later, Taquet (1967, 1969, 1972; Ricqlès, 1969) announced the discovery of *Moradisaurus* from the Late Permian of Niger based on a lower jaw that differs from all other captorhinids in having nine tooth rows. Although more material of *Hecatogomphius* has not been forthcoming, *Moradisaurus* is also represented by good skull (Ricqlès, 1969) and postcranial material as yet undescribed.

Table 2 summarizes current knowledge of captorhinid distribution. Although all but one (*Protocaptorhinus*) of the post-Early Permian captorhinids are members of Group 6, this one exception is enough to contradict the coincidence of phylogeny with stratigraphy in this case (fig. 6). Other than hypothesizing the widespread nature of primitive as well as ad-

vanced captorhinid taxa, there seems to be little of significance in the distribution as known at present.

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